

the female, but the black marks in the feathers of the breast are absent.

The males begin to get the plumage of the adult when about five or six months old, in such a way that, for instance, birds bred in May are indistinguishable from the old birds in January. In the young males the first change is that the throat becomes black.

The females also acquire the spots on the underside at the same period.

Although the males have not exactly an eclipse plumage, they yet go back in colour a good deal after the breeding-season, and, for a while, the bright colours are clouded over—even the white spots are less bright.

I have a flock of fifteen birds, and have bred them during three or four years, with the result as described above.

XI.—*Bird-parasites and Bird-phylogeny**.

By LAUNCELOT HARRISON, B.Sc.

(Text-figure 5.)

I HAVE always had the intention of, sooner or later, bringing under the notice of ornithologists the trend of my work upon bird-parasites, and I am very sensible of the privilege which is mine in being asked to address the Club this evening. All field-ornithologists are very well aware of the existence of the Mallophaga, or Biting Lice, of which by far the greater number are distributed upon birds, although they are also found upon nearly all families of mammals. But few, I think, realise how innumerable are the species of these bird-parasites, and what a field they open up for the study of a fascinating side-light on ornithology. It is to this side-light, this oblique illumination of ornithology, that I wish to direct your attention.

* An address, opening a discussion on this subject, delivered to the British Ornithologists' Club on January 12, 1916.

I do not wish to thrust any wearisome entomological details upon you, but, for the purposes of the thesis which I propose to develop, I must outline a very few facts—first, as to the relations and, secondly, as to the biology of these insects.

The Mallophaga are an order of minute insects, ranging in length from one to, in a few exceptional cases, upwards of ten millimetres, the average being about two millimetres. They find their nearest relatives, among free-living insects, in the Psocids, or Book Lice; while they are still more intimately related to another parasitic group, the Anoplura, or Sucking Lice. They are divisible into two suborders: a more primitive one in which the antennæ are hidden beneath the head, and in which the tarsi carry two functional claws; and a more specialised one, in which the antennæ project freely laterally, and which has but one functional claw upon the tarsus. These suborders are, respectively, the Amblycera and the Ischnocera.

The Mallophaga are completely parasitic in all stages of their life-history. Eggs are laid upon the feathers of the host; this gives rise to a larva, generally similar to the adult, and which passes by successive moults through two later larval stages to the adult condition. The insects feed upon feather-barbules and epidermal detritus, and are incapable of maintaining life for more than a couple of days off the body of the host. The Amblycera, the more active suborder, usually leave the host upon its death; and, as it is only under very exceptional cases that they can find a new host, perish altogether. The Ischnocera fix themselves by their mandibles to the feathers of the host, and die *in situ*. Transference from host to host can, then, only take place during actual contact, either at mating, or from brooding mother to young, or, in the case of gregarious birds, when roosting together, or on rare occasions of accidental contact.

Owing to the fact that these insects have lived for a very long time under very equable conditions, on a nutriment of

epidermal products which varies little in chemical composition, at a body temperature which remains practically uniform, and without any complication of the nature of a struggle for existence, they exhibit a condition that I have elsewhere referred to as "retarded evolution." They have not evolved as fast as their hosts. The Pigeons of the world include a very varied assemblage of birds, ranging from large, almost flightless, forms, such as *Goura*, to tiny Doves such as *Stictopelia*. They are parasitized by species of Mallophaga belonging to five genera, two of Amblycera and three of Ischnocera. In connection with one of the latter, *Lipeurus*, we have the remarkable phenomenon of *L. columbae*, passing for the present as a single species, occurring on practically all the Pigeons of the world; while the remaining genera from Pigeons, though they have produced a considerable number of species, nevertheless present a very distinct facies which enables us to detect them as Pigeon-parasites, even when taken straggling upon other hosts. The same thing holds true for any other group of birds. Parasites of Crows, of Kingfishers, of Hawks, of Plovers, of Petrels, are recognisable as such, whether their host origin be known or not.

This condition can have only one reasonable explanation. Just as everyone in this room is convinced that each of the larger groups of birds has been derived from one common ancestral stock, so we must believe, if we examine the evidence in more detail than I am able to submit to you to-night, that the parasites of these groups have also evolved from the parasites of the ancestral stock. And the point I wish to impress upon you is, that they have evolved at a slower rate.

This statement implies that the Mallophaga took to a parasitic mode of life at a very early period, and I wish to suggest to you the grounds upon which I base my opinion. Upon the marsupial fauna isolated in the Austro-Malayan region occurs a family of Amblycera, of primitive two-clawed parasites, which is very closely related to the lowest and most generalised bird-infesting genera. No member of the

higher suborder occurs upon marsupials. But the parasites of the higher mammals belong, with the exception of a couple of species found upon rodents in South America, to a family of Ischnocera, to the more specialised suborder. I suggest, in explanation of these facts, that Amblyceran Mallophaga parasitized birds and marsupials before the higher mammals had differentiated out, and that the parasitic history of the group dates from late Jurassic or Cretaceous times. No Mallophaga have yet been taken from American marsupials, but I am confident that they will be, and I am equally confident that they will prove to be very closely related to the Boopidæ of Australian marsupials. I do not ask at present any acceptance for my very speculative statement, but I believe that it will be justified when descriptions of forms from American marsupials are available. For my present purpose, I am content to come to much more recent times, and to something upon which I can offer you more substantial evidence. The Ostriches and the Rheas are separated upon two different continents. They possess Ischnoceran parasites—that is to say, parasites of the higher suborder,—which are distinguished from all other Mallophaga by a peculiar asymmetry of the chitinous framework of the head, an asymmetry that can be of no use to the insects. It is very certain that these parasites have had common origin, a fact which not only affords additional evidence of the common origin of the host groups, but which also allows us to set the acquisition of the parasitic habit by the Mallophaga sufficiently far back for all practical purposes. The more specialised suborder was leading a parasitic life at such time as the original Struthious stock became split in two, and the two halves isolated in the Ethiopian and Neotropical regions.

I wish to touch upon just one more point before I proceed to apply the statements I have already made. I have shown that the general condition of Mallophagan distribution cannot be zoo-geographical, but is, rather, a distribution according to host. Birds of any family, whether at the pole

or the equator, in the Old World or New, carry the same types of parasite. I have shown that opportunities of invading a new host are limited. The final question I wish to discuss is: Whether it is possible for parasites to reach and thrive upon hosts not of their proper group, and so to vitiate any general theory based upon their distribution? I admit freely that they can invade, and have invaded, other than their true hosts, and I admit that they can thrive upon these new hosts. Bird-parasites have been found living upon mammals, marsupial parasites on carnivores; a species of the Petrel type, undoubtedly originally parasitic upon Petrels, has become established as a normal parasite of Skuas; *Gonicotes gigas*, a parasite of the genus *Numida*, will be found on domestic Fowls almost anywhere. But I submit that these cases are few, and are almost always capable of detection.

I have now put before you the main points to which I wish to direct your attention, and I will briefly recapitulate them. The Mallophaga are a group of insects with a long-standing history of parasitism, which, from their biological conditions, have tended to be handed down from parent to offspring in such a manner as to be associated always with definite host groups, and which have evolved at a much slower rate than their hosts. These facts made it quite evident to me, when I began some six years ago to work at Mallophaga, that the group should be useful in connection with the very vexed question of bird-phylogeny.

I am sure that, even in a gathering of ornithologists, I may say that very little is known about the inter-relations of the bird orders. We can easily divide birds up into a number of perfectly natural groups, but I think that few in this room would care to answer the question as to whether a Crow, say, was more nearly related to a Hawk or to a Duck. Ordinary morphological and embryological methods have broken down badly as far as birds are concerned, and the fossil record is woefully inadequate. This is my excuse, if excuse be required, not for attempting to classify birds

by their parasites, for I know that that would be absurd, but for putting forward the clues as to affinity which these parasites seem to afford. Such clues may, at all events, help the morphologist to attack his problem in a new light, and to separate those characters of phyletic value from the rest.

I cannot at present, even if the brief time at my disposal allowed, put before you a great deal in the way of positive results of this line of investigation. The Mallophaga themselves have to be more thoroughly collected, examined, and understood before a complete statement can be attempted. But I will just mention a few suggestions I have already published, and finish by giving you a preliminary result of an actual attempt to indicate a natural classification of the Tubinares by means of some of their parasites.

I have already shown elsewhere that Tinamous, Fowls, and Pigeons possess in common Mallophaga of the very distinct family Gonioididæ, and are not infested by the family Philopteridæ. These birds are very generally admitted to be closely related, and parasitic evidence supports this view. *Opisthocomus* also possesses a Gonioidid parasite, which helps to confirm its suggested Gallinaceous affinities. But the same conditions, presence of Gonioididæ and absence of Philopteridæ, obtain with the Penguins. No one has ever suggested any affinity between the Penguins and the Galliform complex, but the evidence afforded by the parasites would seem to demand such affinity.

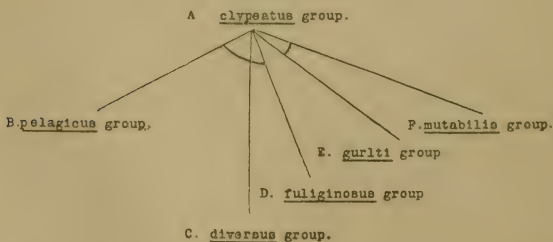
I have shown that the Mallophagan parasites of the Palamedeidæ link up with those of Ducks, Geese, and Swans, thus confirming the Anserine affinities of this somewhat anomalous group. I have suggested, upon the same basis, that the Rails form a very distinct group, of at least ordinal rank; that the Parridæ are Rails, not Limicolines; and, finally, that the Apterygidæ are more nearly akin to the Ralli than to any other living birds, and have nothing in common with the other Ratitæ. Of the latter, the Ostriches and Rheas would seem to have certainly originated from a common ancestral stock, from which I believe the

Emeus also to have been derived, though the evidence here is not quite so convincing.

So much for the few suggestions I have already put forward in print. As I have said already, much more will have to be known about the Mallophaga themselves before any general results can be adduced. But the following attempt will serve to illustrate both my ideas and their possibilities.

The genus *Lipeurus* contains a great number of species found upon nearly all bird families. The *Lipeuri* of Petrels exhibit a very distinct facies, with the details of which I need not trouble you, but which renders them easily recognisable at a glance as Petrel parasites. They fall into six well-marked groups, which may easily be distinguished by the structure of the head. These six groups I name after the best-known species in each of them, the *clypeatus*, *pelagicus*, *diversus*, *fuliginosus*, *gurlti*, and *mutabilis* groups, but, for our present purpose, it will suffice to distinguish them by the first six letters of the alphabet. The precise inter-relation of these groups is not quite certain. I express it tentatively in the diagram.

Text-figure 5.



The main things that stand out are the distinctness of groups E and F from the remaining four, though they show indications of derivation from the *clypeatus* (A) type. Group A is also distinct; groups B and C fairly close

together, while group C shows a remarkable parallelism with group D.

If I now group under the six headings indicated the genera of Petrels from which I have parasites, the following lists result:—

A.	B.	C.
<i>Garrodia.</i>	<i>Procellaria.</i>	<i>Æstrelata.</i>
<i>Oceanites.</i>	<i>Pelagodroma.</i>	<i>Puffinus.</i>
<i>Oceanodroma.</i>		<i>Priofinus.</i>
	<i>Pelecanoïdes.</i>	<i>Majaqueus.</i>
D.	E.	F.
<i>Æstrelata.</i>	<i>Fulmarus.</i>	<i>Fulmarus.</i>
<i>Puffinus.</i>	<i>Thalassæca.</i>	<i>Priocella.</i>
<i>Priofinus.</i>	<i>Pagodroma.</i>	<i>Ossifraga.</i>
<i>Majaqueus.</i>	<i>Priocella.</i>	<i>Diomedea.</i>
	<i>Daption.</i>	<i>Thalassogeron.</i>
<i>Prion.</i>		<i>Phæbetria.</i>

I have already remarked on the degree of affinity between the group of parasites, which fall into three divisions, A—BCD—EF. Re-arranging the genera in these three divisions, according to the parasite groups, we have the following:—

A.	B.	E.
<i>Garrodia.</i>	<i>Procellaria.</i>	<i>Daption.</i>
<i>Oceanites.</i>	<i>Pelagodroma.</i>	<i>Pagodroma.</i>
<i>Oceanodroma.</i>		<i>Thalassæca.</i>
	<i>Pelecanoïdes.</i>	
	CD.	EF.
	<i>Æstrelata.</i>	<i>Fulmarus.</i>
	<i>Puffinus.</i>	<i>Priocella.</i>
	<i>Priofinus.</i>	
	<i>Majaqueus.</i>	F.
		<i>Ossifraga.</i>
	D.	<i>Diomedea.</i>
	<i>Prion.</i>	<i>Thalassogeron.</i>
		<i>Phæbetria.</i>

Before proceeding to compare the classification thus arrived at with any other that has been proposed, I should like to lay particular stress on the fact that it has been arrived at *without any consideration whatever of the Petrels themselves*, purely from a study of one genus of parasites, and that it was constructed before I had consulted any ornithological classification of the group.

I now give for comparison the classification of Forbes ('Challenger' Reports, Zoology, iv. 1882):—

OCEANITIDÆ.		PROCELLARIIDÆ.	
		PROCELLARIINÆ.	DIOMEDEINÆ.
α.	{	β.	{
		δ.	{
ζ.	{		

The correspondence between the two schemes is certainly remarkable. My evidence points to *Pelagodroma* belonging to the *Procellaria*, not to the *Garrodia* group; to the Fulmars being nearer to the Albatrosses than to the Shearwaters; and to *Ossifraga* being an Albatros rather than a Fulmar; but in all other respects the schemes coincide.

There is not time for me to discuss my results in detail, or to do much in the way of comparison with other classificatory schemes. But I would point out that, though my

material from *Pelecanoides* is very limited, it, nevertheless, does not support the isolated position usually given to this genus. Considering such a classification as that in Sharpe's 'Hand-list,' my confirmation of Forbes's general position indicates that the small Petrels are quite wrongly included in a single family; that such genera as *Thalassœca*, *Priocella*, and *Pagodroma* are Fulmars, not Shearwaters; and that *Prion* is not a Fulmar, but is nearer to the Shearwaters. I have no material from *Fregatta*, *Bulweria*, *Halobœna*, and one or two other rare genera, so can say nothing about them.

I think that the illustrations I have put before you will suffice to show that there is something in my ideas, and that, when I have as plentiful a material to argue from in other groups as I have had in the Petrels, I may be able to give you some useful indications. And, in closing, I would take this opportunity of appealing to those ornithologists who may be undertaking expeditions themselves, or who have collectors in the field, to have these insignificant parasites carefully collected, and placed where they may render service to the science of ornithology, a science in which I may claim to be interested as deeply as yourselves.

[NOTE.—Since the above was written, I have been able, through the kindness of Mr. W. R. Ogilvie-Grant, to examine for parasites some Petrel skins in the British Museum. The results show that *Pelecanoides* holds a much more isolated position than I have allowed, but at the base of the Shearwater group, that *Bulweria* goes with the Shearwaters, and that *Halobœna* may be bracketed with *Prion*.—L. H. 31. i. 16.]